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Research Article

Effects of earthworm invasion on soil properties and plant diversity after two years of field experiment

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Abstract

Although belowground invasive species are probably equally widespread and as important as their aboveground counterparts, they remain understudied, and their impacts are likely to be stronger when these invaders act as ecosystem engineers and differ functionally from native species. This is the case in regions historically devoid of native earthworms, such as parts of northern North America, which are now experiencing an invasion by European earthworms. Although invasive earthworms have been reported to have multiple consequences for native communities and ecosystem functioning, this knowledge is mostly based on observational studies, and the mechanisms underlying their cascading impacts need to be investigated. Here, we thus investigated the sequence of events, i.e., ecological cascades following earthworm invasion, that have rarely been studied before, in a two-year field experiment. We expected that the changes in soil abiotic properties observed following invasion would coincide with changes in plant community diversity and community trait composition, as well as in alterations in above- and belowground ecosystem functions. To test these hypotheses, we set up a field experiment that ran for two years in a forest in Alberta (Canada) to investigate soil properties and understory plant community composition in response to invasive earthworms.

Our study shows that invasive European earthworms alter several soil abiotic properties (i.e., soil nutrient content, and pH) after two years of experiment. Invasive earthworm effects varied with soil depth for some soil properties (i.e., soil pH, water-stable aggregates, nitrogen, and microbial basal respiration), but we did not find any significant earthworm effect on soil water content, bulk density, or the total soil microbial biomass independently of the soil layer. Moreover, invasive earthworms did not affect plant community composition and only slightly affected community diversity in this short-term experiment. The minor changes observed in plant functional group composition are thus potentially the first signs of invasive-earthworm effects on plant communities.

Our research provides experimental evidence that previously reported observational effects of invasive earthworms on soil properties are indeed causal and already significant after two years of invasion. These changes in soil properties are likely to have cascading effects on plant community composition, functional diversity, and ecosystem functioning, but such effects may take longer than two years to materialize.

Key words: Biological invasion, detritivore, ecosystem engineer, microbes, plant functional traits, soil nutrients

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Introduction

Worldwide biodiversity loss is driven by climate change and anthropic activities, such as habitat fragmentation or pollution, and threatens ecosystem functions and processes (Wardle et al. 2011; Cardinale et al. 2012; Hooper et al. 2012). Biological invasions are also ranked as significant biodiversity threats (Sala et al. 2000; Murphy and Romanuk 2014; IPBES 2019), and there is a growing interest in understanding the effects of invasive species on native biodiversity, the underlying mechanisms of these effects, and in evaluating the costs of their management (Vilà et al. 2011; Simberloff et al. 2013; Vilà and Hulme 2017; Renault et al. 2022; Turbelin et al. 2023).

Although still understudied, belowground invasive species are probably equally widespread and as important as aboveground invasive species (Ehrenfeld and Scott 2001; Hendrix 2006). The effects of these invasive species on native communities and ecosystems are likely to be stronger when the invasive species act as ecosystem engineers (Jones et al. 1994) and when they are functionally dissimilar to the native community (Wardle et al. 2011). A prominent example is European earthworms that invade previously earthworm-free regions of the North-American continent. These earthworm-free regions, such as the eastern and mid-western parts of the USA and the Rocky Mountains in Canada (James and Hendrix 2004; Addison 2009; Hendrix et al. 2008), have been largely devoid of native earthworms since the last glaciation (Bohlen et al. 2004; Hendrix et al. 2008) but are currently facing an ongoing invasion by European earthworms (Bohlen et al. 2004; Hendrix et al. 2008) and, more recently, by Asian jumping worms (Chang et al. 2021). There, invasive earthworms have multiple consequences for native communities and ecosystem functioning (Frelich et al. 2019).

The effects of invasive earthworms on native ecosystems can result from changes in the physical and chemical properties of the soil due to their feeding and burrowing activities. These impacts will depend on the identity and ecological group of the earthworm species, as the different ecological groups have different behaviors (Bouché 1977), and thus on the earthworm community composition (Ferlian et al. 2018, 2020). Invasive European earthworms were shown to remove the soil surface litter and reduce the organic matter in the topsoil horizons (Hale et al. 2005; Resner et al. 2015). Moreover, their activities decrease the soil water content (Larson et al. 2010), but increase soil denitrification (Jang et al. 2022) and the leaching of soil nutrients (Bohlen et al. 2004; Frelich et al. 2006). They consequently change the nutrient availability and distribution in forest soils (Shuster et al. 2001; Bohlen et al. 2004; Resner et al. 2015), with effects potentially depending on if it is the organic or the mineral soil layer considered (Fahey et al. 2013a, 2013b; Ferlian et al. 2020). Another explanation of the impacts of invasive earthworms on ecosystem functioning could be their direct or indirect effects on other above- or belowground organisms (Frelich et al. 2012, 2019; Jochum et al. 2022).

Indeed, soil microbial communities, aboveground and soil fauna, as well as plant communities, were shown to be affected by invasive European earthworms (McLean et al. 2006; Burtis et al. 2014; Craven et al. 2017; Ferlian et al. 2018; Jochum et al. 2021, 2022; Jang et al. 2022), with many studies focusing on plant communities (Craven et al. 2017). For example, several studies showed that invasive earthworms decreased plant species diversity (Hale et al. 2006; Holdsworth

et al. 2007; Gibson et al. 2013; Drouin et al. 2016; Craven et al. 2017). Their effects seem to depend on plant species and functional group identity (Drouin et al. 2016; Alexander et al. 2022) but, overall, they promote grass species (Frelich et al. 2006; Drouin et al. 2016; Craven et al. 2017). The changes in plant community diversity and composition could be due to several mechanisms, such as the outcome of earthworm-seed/seedling interactions (Eisenhauer et al. 2009a; Drouin et al. 2014; Clause et al. 2015; Nuzzo et al. 2015; Fleri et al. 2021), or result from changes in the soil properties due to invasive earthworms as mentioned above (Ferlian et al. 2020). Such changes could lead to a modification in plant development and plant functional traits (Dávalos et al. 2013, 2015; Cameron et al. 2014; Dobson et al. 2017; Richardson et al. 2018). The redistribution, mineralization, and elevated availability of nutrients due to earthworm activities could favor grasses (Thouvenot et al. 2021; Schwarz et al. 2024) which are more efficient in taking up soil nutrients and are thus considered as resource-exploitative species (Craine et al. 2001; Freschet et al. 2017) and often possess a high specific leaf area and leaf nitrogen content. This would lead to changes in the dominance structure of different plant functional groups, plant community composition, and thus in the overall taxonomic and functional diversity of the plant community, with consequences for plant community trait composition and ecosystem functions (i.e., "mass-ratio hypothesis, Grime (1998)) like plant community productivity and litter decomposition. For example, the biomass of litter would be lower in the presence of invasive earthworms: this would be explained by a faster decomposition process due to the presence of a litter more easily decomposed, induced by the changes in the litter quality (high nitrogen content) following the dominance of graminoid species in the communities of the invaded area that are efficient in taking up plant-available soil nitrogen.

As previously described, there are diverse hypotheses that have been put forward to explain the impacts of invasive earthworms on native biodiversity and ecosystems (e.g., Hendrix et al. 2008; Eisenhauer et al. 2019), but basically all of what we know is based on observational field studies and lab experiments, and there is a need to establish causal links and to understand the specific mechanisms under field conditions (Eisenhauer et al. 2019). Our study thus aims to fill this knowledge gap, by exploring the mechanisms behind plant community and ecosystem function changes after earthworm invasion and investigating potential cascading effects from altered soil properties to plant community composition. Thus, here, to better understand the short-term effects of earthworm invasions, which have rarely been studied under field conditions, we set up a field experiment that ran for two years in a forest in northern North America. We investigated the effects of invasive European earthworms on the soil structure and nutrient content, as well as on soil microbial activity and plant communities, and the associated consequences for ecosystem functions. We hypothesized to observe changes in soil abiotic properties (H1) that would then be associated with a positive effect of invasive earthworms on the cover and taxonomic diversity of grass species (H2). This would result in modifications of the community-weighted mean plant trait values (i.e., a decrease in plant height and an increase in leaf nitrogen content following grass dominance in the plant community; H3). Such changes were expected to coincide with changes in ecosystem functions like an alteration of plant community productivity and soil microbial activity, and an increase in litter decomposition (H4).

Methods

Study area and experimental design

The field experiment was set up in July 2017 in the still non-invaded area of an aspen forest of the Kananaskis Valley (Eisenhauer et al. 2019), in the front range of the Canadian Rocky Mountains (51°02'06"N, 115°03'54"W, Alberta, Canada), and was terminated in June 2019. The description of the climate in the valley, as well as the soil abiotic parameters of the forest can be found in previous studies (Scheu and Parkinson 1994; Eisenhauer et al. 2007, 2009a; Straube et al. 2009; Jochum et al. 2022). In this forest, trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) are the dominant tree species. The understory community is composed of different herbs (e.g., *Aster conspicuus*, *Fragaria virginiana*, *Delphinium glaucum*), grasses (e.g., *Calamagrostis rubescens*, *Leymus innovatus*), legumes (e.g., *Lathyrus ochroleucus*, *Vicia americana*), and woody plant species (e.g., *Rosa acicularis*, *Rubus idaeus*, *Symphoricarpos occidentalis*).

Earthworms are currently invading this forest, and the invasion by earthworms has been studied intensively across the last three decades, which is why there is solid empirical evidence for the proceeding invasion of the forest and the moving invasion front (Scheu and Parkinson 1994; Eisenhauer et al. 2007, 2009a; Straube et al. 2009; Jochum et al. 2022; Thouvenot et al. 2024a). The experiment was established in a non-invaded area of the forest that, based on previous work, would be invaded by the earthworm species that had already been present in this forest within a couple of years. This careful and conservative approach is reflected by the fact that some epigeic earthworms could even colonize some of the experimental control enclosures within the duration of our study (see information below). Notably, our experiment was well communicated with local authorities, and we were granted the required permits (Alberta Environment and Parks; Alberta Tourism, Parks and Recreation Division; Permit number 16–139).

In the non-invaded part of the forest, 20 enclosures (1 × 1 m) were randomly established (Eisenhauer et al. 2019), and were on average 47.8 m (±23.7 m (sd)) apart from each other (distance range: from ~10 m to ~128 m; Fig. 1A). The non-invaded part of the forest was defined on the basis of earthworm abundance data from a comprehensive earthworm sampling campaign where the number of individuals was close to zero (the data published in Jochum et al. 2021; Ferlian et al. 2024). The enclosures consisted of metal sheets (60 cm width, 1 m length) encased in the soil: 20 cm of the metal sheets were above and 40 cm below the soil surface to limit earthworm escape or natural colonization (Fig. 1B).

To establish the enclosures, we used an aluminum frame (1 × 1 m) positioned on the soil surface to demarcate the enclosure boundaries. Then, we dug out the topsoil (~10–20 cm deep) around the undisturbed plot area, before cutting the trenches (~40 cm deep) with a soil trencher along the inner edge of the ditches. The four metal shields were then inserted into the soil to reach 40 cm of soil depth. All ditches, grooves, and holes were then filled with the previously removed soil, before being compacted to restore the soil as much as possible. Velcro outdoor tape (hook part) was attached to the inner side of the shields to prevent earthworms from escaping (as earthworms cannot pass the hook-like structure; Lubbers and van Groenigen 2013).

All earthworms used in the field experiment were taken from the local populations of the study site (Alberta Environment and Parks, Permit number 16–139), and we did not introduce any additional earthworm species. Earthworms were collected in the field using the mustard extraction method (Jochum et al. 2022), washed,

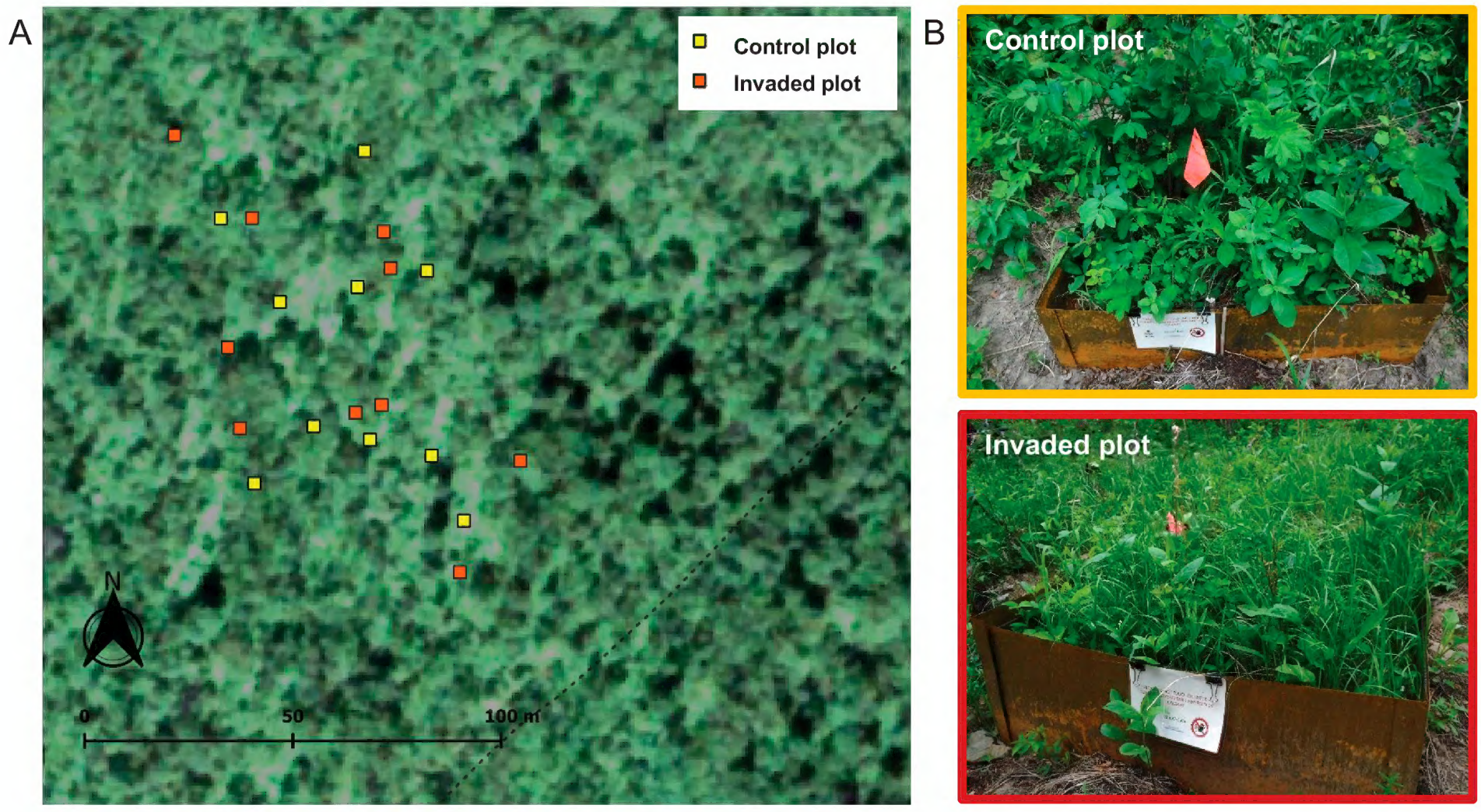

Figure 1. Study site and enclosure set-up. Map (**A**) of the study site located at the north of Barrier Lake, Kananaskis Valley, Alberta, Canada (51°02'N, 115°03'W), with the enclosures (**B**). Colors show the 20 enclosures set-up in the non-invaded area: there are 10 control enclosures (yellow) and 10 invaded enclosures (red). The hiking trail is the black dotted line. Mapping information: coordinate system UTM Zone 11 U, DOP data © government of Alberta 2014, and mapping performed using QGIS 3.30.0 (2023).

and sorted to ecological groups (i.e., epigeic, endogeic, anecic) before being added to the enclosures. We found only four species varying in terms of abundance, and with mainly one species per ecological group, except for epigeic species for which we found two species. This constrained the experimental design/treatment: we thus manipulated the presence *vs.* absence of the invasive earthworm community (i.e., presence *vs.* absence of the three ecological groups of earthworms). This invasion treatment was randomly assigned to each enclosure, with 10 enclosures (replicates) per treatment. Earthworm density added to the enclosures was close to the common medium densities in the area (mean ± sd: 32.9 ± 19.4 g m^{-2} and 42.8 ± 22.7 individuals m^{-2} ; Jochum et al. 2022). We equally distributed the same number of individuals per ecological group and then balanced the total biomass for each enclosure to keep similar biomass among all of the invaded enclosures to control for strong biomass effects observed before (Craven et al. 2017). The earthworm community was composed of the species *Dendrodrilus rubidus* (epigeic), *Dendrobaena octaedra* (epigeic), *Octolasion tyrtaeum* (endogeic), and *Lumbricus terrestris* (anecic). On average, we added ~ 14 anecic individuals (corresponding to a total fresh biomass of ~ 17.6 g m^{-2} on average), 45 endogeic individuals (~ 17.2 g m^{-2}), and 12 epigeic individuals (~ 1.6 g m^{-2}) to each enclosure receiving the earthworm treatment. The earthworms were added on 23rd of July 2017, and we verified the invasion status in all enclosures (i.e., the presence *vs.* absence of the earthworm community) at the end of the field experiment after all measurements by extracting the earthworm community from the 17th to 20th of June, 2019, thus after 694 days of experiment (~23 months). To do so, we assessed the abundance, biomass, and ecological group richness of the earthworm community in one quarter (0.5 × 0.5 m) of each of the enclosures, *via* a combination of hand-sorting and mustard extraction methods

(Ferlian et al. 2022; Jochum et al. 2022). The mustard extraction method is commonly used to estimate earthworm abundance and biomass (Eisenhauer et al. 2007; Straube et al. 2009; Jochum et al. 2022). We found earthworms in all enclosures that received the earthworm treatment but also epigeic earthworms in seven of the control enclosures. This light invasion of the control enclosures could be due to the presence of few individuals, tiny juveniles of epigeic earthworms that occurred at the site before setting up the experiment and are starting to invade the site (as epigeic earthworms are typically the first species to invade a new area). Another explanation would be the natural colonization of the enclosures by epigeic earthworms that are very mobile and might be able to cross the barriers, and/or to the introduction of eggs or individuals by birds or large animals like deer, even if rarely reported. We unfortunately cannot estimate the timing of this invasion of some control enclosures, but despite this colonization, we observed a difference between the two invasion treatments, with a biomass (+11.6%) and ecological group richness (+1.6%) significantly higher (only marginal difference for the earthworm abundance) in the invaded than in the control enclosures (see Suppl. material 1), allowing us to test the effects of earthworm experimental treatment on our focal response variables.

Plant community and plant trait measurements

We visually estimated the cover of each plant species in the twenty enclosures, by using the modified decimal scale from Londo (1976), in June 2019. Thirteen cover categories were defined (i.e., <1%; 1–3%; 3–5%; 5–15%; 15–25%; 25–35%; 35–45%; 45–55%; 55–65%; 65–75%; 75–85%; 85–95%; and >95%), and we used the median values of the categories to calculate the relative abundance of the plant species. Then, plant functional traits were measured on the dominant plant species of each enclosure. In other words, for each enclosures, we listed all the plant species that were the most dominant until reaching a collective minimum total cover of 80% of the enclosure (Pakeman and Quested 2007), and measured traits on these species following standard protocols (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2016). We measured the vegetative height (cm) of the dominant species in each enclosure, by selecting three individuals, if possible. The height was defined as the shortest distance between the soil and the top leaf. After measuring the height, we assessed the nutrient content of the leaves (carbon and nitrogen) on two individuals per species per enclosure. To do so, we collected and pooled two leaves per individual. However, in cases of low species abundance, we measured the traits on a reduced number of individuals, thus sometimes on only one individual, when this individual represented a high percentage of cover of the enclosure, to avoid missing any important components of the plant community. Leaves were treated as a whole, without separating leaflets or petioles for herbs, legumes, and woody plants; while for grasses, only the laminae were considered. Each pool of leaves was dried individually at 60 °C for at least three days, before being ground, using liquid nitrogen when necessary. Samples were then put into tin capsules prior to the analyses of leaf carbon and nitrogen content (% dry-leaf mass). The nutrient analyses were performed using 3.5 to 5 mg of dry weight by combustion with an elemental analyzer (Vario EL III, Elementar Analysensysteme GmbH, Hanau, Germany).

Additionally, plant functional group-specific biomass was measured in a quarter of each enclosure (0.5 × 0.5 m). Plants were harvested by cutting the shoots at the soil surface level and later sorted in the laboratory according to their functional group (i.e.,

herbs, grasses, legumes, and woody plants). If not processed immediately, the bags with biomass were stored air-tight in a fridge at 4 °C before being processed (within a maximum of two days after collection). The plant samples were then dried at 60 °C for at least 72 h and weighed to assess plant biomass. We acknowledge that some plant species harvested were not observed during the visual estimation of species-specific plant cover performed earlier, and thus to account for them in the calculation of plant α-diversity indices, we assigned them a cover of 0.5%. Plant community productivity was calculated by summing up the dry biomass of the different plant functional groups.

Soil and ecosystem properties

Soil abiotic and biotic properties were assessed in one quarter next to the one used to measure plant functional group biomass, while litter biomass and canopy openness were measured at the enclosure level.

One soil core (depth 10 cm; diameter 5 cm) was sampled to get information about soil abiotic (e.g., pH, nutrients, water content) and biotic properties (e.g., microbial biomass and basal respiration). Ecological as well as mineralization processes and nutrient contents typically decrease with soil depth, with the strongest decrease typically happening in the upper 10 cm (Chen et al. 2021), and in the organic layer that represents, on average, the first 5 cm in this area (Thouvenot et al. 2024a). Thus, each soil core was split into two depth layers (0–5 cm and 5–10 cm depth). Each layer of soil samples was stored at 5 °C until being processed in the laboratory. Then, they were sieved (2 mm) and stored afterward at -20 °C until further analyses. A sub-sample of this sieved soil was taken, dried at 60 °C for 72 h, and ground. Then, around 20 mg of dry weight per sample was put in a tin capsule for soil nutrient analysis that was performed with an elemental analyzer (Vario EL Cube, Elementar Analysensysteme GmbH, Hanau, Germany).

The fresh soil samples (2 g for the 0–5 cm depth and 10 g for the 5–10 cm depth) were air-dried and then dissolved in 12.5 ml 0.01 M $CaCl_2$ solution for the upper layer and in 25 ml 0.01 M $CaCl_2$ solution for the deeper soil layer. After shaking the solutions, they were left for at least 1 h before the pH measurements were taken. The pH was determined using different subsample sizes as the upper soil layer soaked most of the $CaCl_2$ solution: we had to change the ratio between the soil mass and volume of solution used to be able to measure the pH of the soil solution, and statistical analyses were performed on each soil layer separately.

Soil microbial activity was measured for each soil layer, using 2 to 4 g of fresh soil using an O_2-microcompensation apparatus (Scheu 1992). We measured soil microbial basal respiration (µl O_2 h^{-1} g^{-1} dry soil) every hour for 24 h at 20 °C and calculated microbial biomass (Cmic; µg C g^{-1} dry soil) from the maximum initial respiratory response after the addition of glucose, as done before (e.g., Eisenhauer et al. 2007). Substrate-induced respiration was calculated after measuring the respiratory response to the addition of D-Glucose in excess (i.e., to the addition of 8 mg of glucose per gram of soil dry mass, diluted in 0.25 ml of deionized water).

For measurements of soil aggregate stability, a stable 200 ml container was filled per enclosure with soil from a depth of 0–10 cm. Soil was sampled by carefully digging with a hand-spade and discarding soil particles from the rim of the pile to avoid including soil that was compacted during the procedure. Samples were stored in a cooling bag in the field and dried at 60 °C for 72 h in the lab to terminate microbial processes. Water-stable aggregates were separated from unstable ones using the method

described by Kemper and Rosenau (1986). The three measurements of water-stable aggregate per soil layer per enclosure performed were averaged for further analyses.

Soil bulk density was measured in November 2019, in half of the enclosures (5 replicates per treatment), with a 5-cm-diameter soil corer, to a depth of 10 cm. After removal of litter and woody debris, plants were cut off just above the soil surface. Soil cores were then taken, transported to the lab, and weighed fresh before drying them for 24 h at 105 °C and weighing them again to the nearest 0.01 g. Soil bulk density was then calculated as g dry weight per m^3.

Moreover, the litter was collected on the same quarter used to measure plant functional group biomass, and this litter biomass was multiplied by four to represent the whole enclosure. We complemented this litter collection with the litter biomass collected *via* suction sampling to get a measure of total litter biomass per m^2. Suction sampling was performed on the whole enclosure, after plant community trait measurements and aimed to sample vegetation and ground fauna, (unpublished data). Here, we used the litter biomass to get an estimation of the litter decomposition. We estimated the canopy openness (%) i.e., the percentage of open sky, for each enclosure by taking pictures with a cell phone (iPhone 6S Plus+) and an Olloclip FishEye lens, on a tripod at a height of 1.4 m. The hemispheric pictures were processed with the WinScanopy software (Régent Instruments Inc., Québec, QC, Canada) to calculate canopy openness.

Statistical analysis

All statistical analyses and figures were performed with R software version 4.3.1 (R Core Team 2023). The effects of the earthworm invasion treatment were tested on soil abiotic properties (i.e., soil carbon and nitrogen content, soil pH, water-stable aggregates and water content) and soil microbial activity (i.e., basal respiration and microbial biomass) using linear models of the package "stats" with Type III F-tests from the package "car" (Fox and Weisber 2019), with the earthworm invasion treatment and the soil depth as factors tested alone and in interaction. The effect of the earthworm treatment on the bulk density (measured in one soil layer), and on pH (different methods used for each soil layer as explained above) were analyzed using linear models with Anova Type II F-tests, as the model did not include the interaction.

To check for changes in plant community composition in response to our treatment, we performed a non-metric multidimensional scaling (NMDS) analysis, with the function metaMDS from the "vegan" package (Oksanen et al. 2019) using Bray-Curtis distances square root transformed. We tested the difference between earthworm treatments using permutational multivariate analysis of variation (Permanova) after 1000 permutations on the square root transformed distances, using the adonis2 function from the "vegan" package (Oksanen et al. 2019).

To characterize the plant community, three α-diversity indices were calculated for each enclosure and each plant functional group: the species richness, the Shannon diversity and Pielou's evenness. They were calculated using the functions *specnumber* and *diversity* from the "vegan" package (Oksanen et al. 2019). In addition, we calculated the community-weighted means (CWMs) (Lavorel et al. 2008) of the plant height, leaf carbon, and nitrogen content for each enclosure, based on the mean trait values per species per enclosure, weighted by the relative median cover of the plant species in this same enclosure, using the function *weighted.mean* from the "stats" package. The effects of earthworms on α-diversity indices calcu-

lated at the community level, on CWM of traits as well as on plant productivity and litter biomass were tested using linear models with Type II F-tests, with the earthworm treatment as a two-level factor and canopy openness as a covariate. The different variables estimated at the plant functional group level were tested using linear models with Type III F-tests: the fixed effects were the earthworm treatment and the plant functional group alone and in interaction, while canopy openness was also specified as a covariate. When the interaction between the plant functional group and earthworm treatment was significant, pairwise comparisons with Holm correction were performed by plant functional group and by earthworm treatment using the package "emmeans" (Lenth et al. 2020).

Model diagnostics were performed using the R base function plot(): the normality of residuals, the homogeneity of variance, and the presence of outliers or influential data points were checked by visual inspection. When necessary, variables were log-transformed ($\log_2$ [x +1]) to meet model assumptions, such as for the plant community productivity, as well as the richness, and relative cover at the plant functional group level, the litter biomass, the soil carbon and nitrogen content, as well as the soil microbial biomass, basal respiration, and dry bulk density. Only soil pH and relative plant functional group biomass were square-root transformed. One data point that stood out in diagnostics plots and with a Cook's distance > 0.5 was removed for soil microbial respiration (Control area, Enclosure 18, soil depth 0–5 cm, Basal respiration value = 0.00). The percentages of change were calculated using estimated marginal means (back-transformed when necessary) from the "emmeans" package. All figures were made with the package "ggplot2" (Wickham 2016).

Use of Artificial Intelligence technologies statement

During the writing process, we used ChatGPT in order to check grammar and spelling, and re-phrase some sentences, but reviewed and edited the content for the manuscript.

Results

Effects of the invasive earthworm treatment on soil abiotic properties

The soil water and carbon content were significantly lower in the deeper soil layer than in the upper soil layer ($F_{1.36}$=32.33, p<0.001, $F_{1.36}$=64.37, p<0.001 respectively, Fig. 2A, B). The earthworm treatment reduced the soil carbon content from 12.2% to 9.6% on average (-21.1%, $F_{1.36}$=4.65, p=0.04), while the soil nitrogen content decreased by 25.8% with the earthworm treatment in the upper soil layer (from ~1.4% of carbon in the control to ~1% in the earthworm treatment) but remained similar in the deeper soil layer (Interaction effect: $F_{1.36}$=4.53, p=0.04, Fig. 2C). Soil pH increased in the deeper soil layer with values ranging from 5.4 in the control treatment to 5.9 in the invasion treatment (+ 8.9%; Earthworm effect: $F_{1.18}$=7.66, p=0.013; Fig. 2D), but it did not change due to earthworm treatment in the upper soil layer (Earthworm effect: $F_{1.18}$=2.05, p=0.17). Moreover, the earthworm treatment did not affect soil bulk density significantly (Earthworm effect: $F_{1.8}$=0.05, p=0.82; Fig. 2E), while the percentage of water-stable aggregates was significantly affected by the interaction between earthworm treatment and soil layer ($F_{1.36}$=5.19, p=0.03, Fig. 2F). The significant difference in soil aggregate stability between soil layers (difference of 11%) in the control treatment was reduced in the

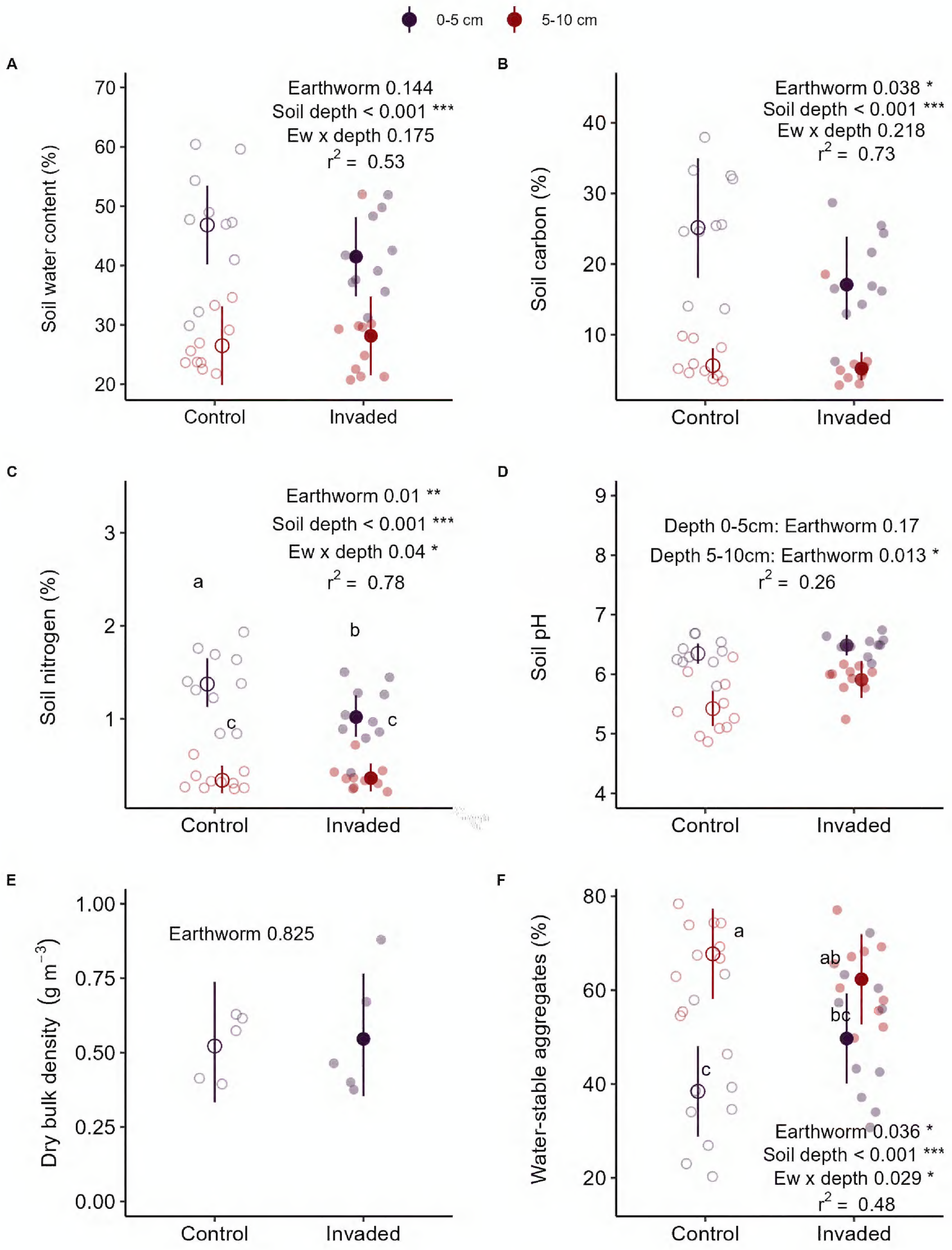

Figure 2. Effect of invasive earthworms on soil abiotic properties. Soil water content (**A**), carbon (**B**) and nitrogen (**C**) contents, pH (**D**), as well as dry bulk density (**E**), soil aggregate stability (**F**), according to the earthworm treatment (control (open circle) vs invaded (filled circle)) and soil depth (0–5 cm (dark gray) vs 5–10 cm (brown), except for the bulk density). Estimated marginal means and confidence intervals $CI_{95\%}$ are shown (after being back-transformed when necessary), while data points are included in the background. The p-values and r^2 are based on linear models. r^2 are given when at least one factor alone or in interaction was significant. Letters correspond to the results of post hoc tests performed when the interaction between earthworm treatment and soil depth was significant: different letters show significant differences between soil depth and earthworm invasion status. Number of observations per earthworm treatment and soil depth: 10 (5 for dry bulk density). Significance codes: ***<0.001; *<0.05.

earthworm treatment (difference of 5% of water-stable aggregates between layers). This effect was probably due to the simultaneous increase of soil aggregate stability in the deeper soil layer (+29.3%), and the decrease (-8%) in the upper soil layer.

Effects of the experimental earthworm invasion on plant community diversity, structure, and trait composition

The Permanova did not show any significant shift in the composition of the plant community in response to the earthworm treatment ($F_{1.18}$=0.86, p=0.76, see Suppl. material 2). Moreover, the α-diversity indices measured at the plant community level were also not affected by the canopy openness, nor the invasive earthworms treatment that did not significantly change plant species richness ($F_{1.17}$=0.001, p=0.97; Fig. 3A), Shannon diversity ($F_{1.17}$=0.37, p=0.55; Fig. 3B), and evenness ($F_{1.17}$=0.84, p=0.37; Fig. 3C) of the community.

Furthermore, our study shows few effects of the earthworm treatment, but significant effects of the plant functional group identity on the plant functional group indices. The plant functional group relative cover ($F_{3.71}$=37.10, p<0.001), richness ($F_{3.71}$=121.36, p<0.001), Shannon diversity ($F_{3.71}$=76.50, p<0.001), and relative biomass ($F_{3.71}$=17.75, p<0.001), but not the evenness ($F_{3.69}$=0.62, p=0.60), were significantly affected by the plant functional group identity. Overall, herbs had the highest relative biomass, cover, richness, and Shannon diversity, while legumes had the lowest. The grasses had similar relative biomass to herbs. Canopy openness increased plant functional group Shannon diversity ($F_{1,71}$=8.02, p=0.006), evenness ($F_{1,69}$=8.39, p=0.005), and slightly the richness ($F_{1,71}$=3.16, p=0.08), but not the relative cover ($F_{1,71}$=2.43, p=0.12) and relative biomass ($F_{1,71}$=0.11, p=0.74). The earthworm treatment alone or in interaction did not affect the relative cover of the plant functional groups ($F_{1.71}$=0.05, p=0.83 and $F_{3.71}$=0.20, p=0.90 respectively, Fig. 4A), nor their relative biomass ($F_{1.71}$=0.04, p=0.85 and $F_{3.71}$=0.02, p=1 respectively, Fig. 4B) or their richness ($F_{1.71}$=0.50, p=0.48 and $F_{3.71}$=1.94, p=0.13 respectively, Fig. 4C). However, the interaction between earthworm treatment and plant functional group marginally affected Shannon diversity ($F_{3.71}$=2.16, p=0.10; Fig. 4D), with this effect mainly driven by a marginally significant increase in the Shan-

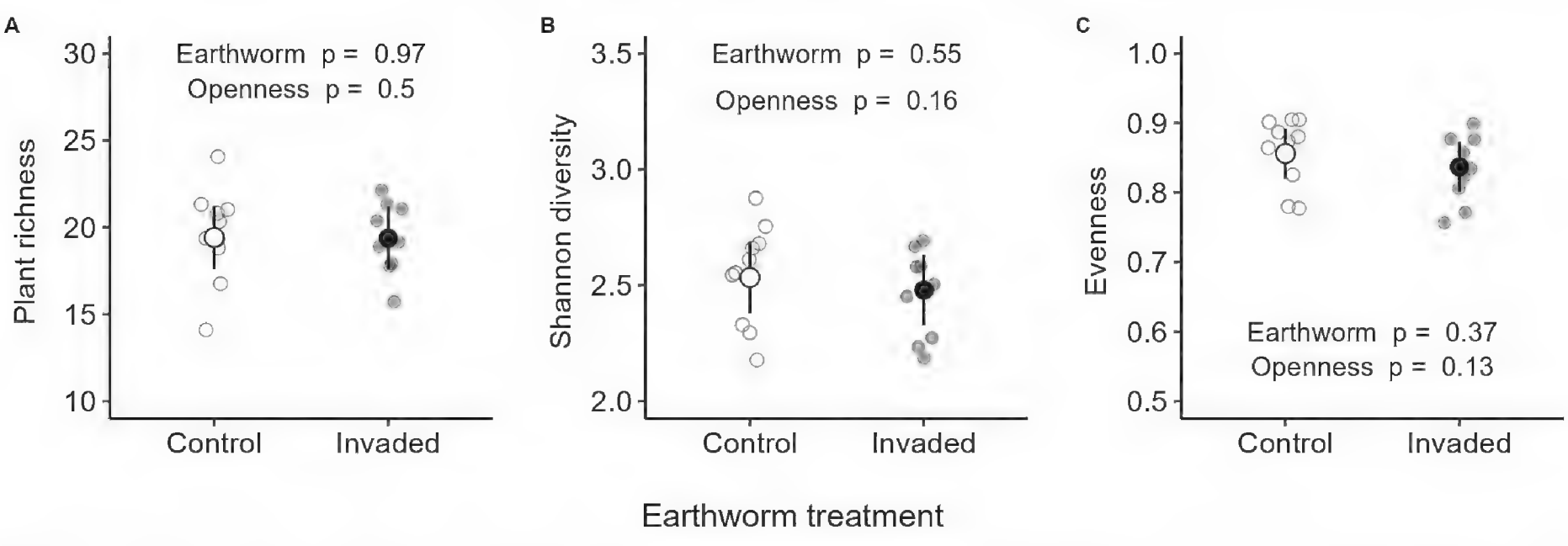

Figure 3. Effect of invasive earthworms on plant community diversity. Comparison of the plant community composition based on the plant richness (**A**), Shannon diversity (**B**), and evenness (**C**) according to the earthworm treatment of the enclosures (control (open circle) versus invaded (filled circle) enclosures). Estimated marginal means and confidence intervals $CI_{95\%}$ are shown (after being back-transformed when necessary), while data points were included in the background. The p-values are based on linear models. Number of observations per earthworm treatment: 10.

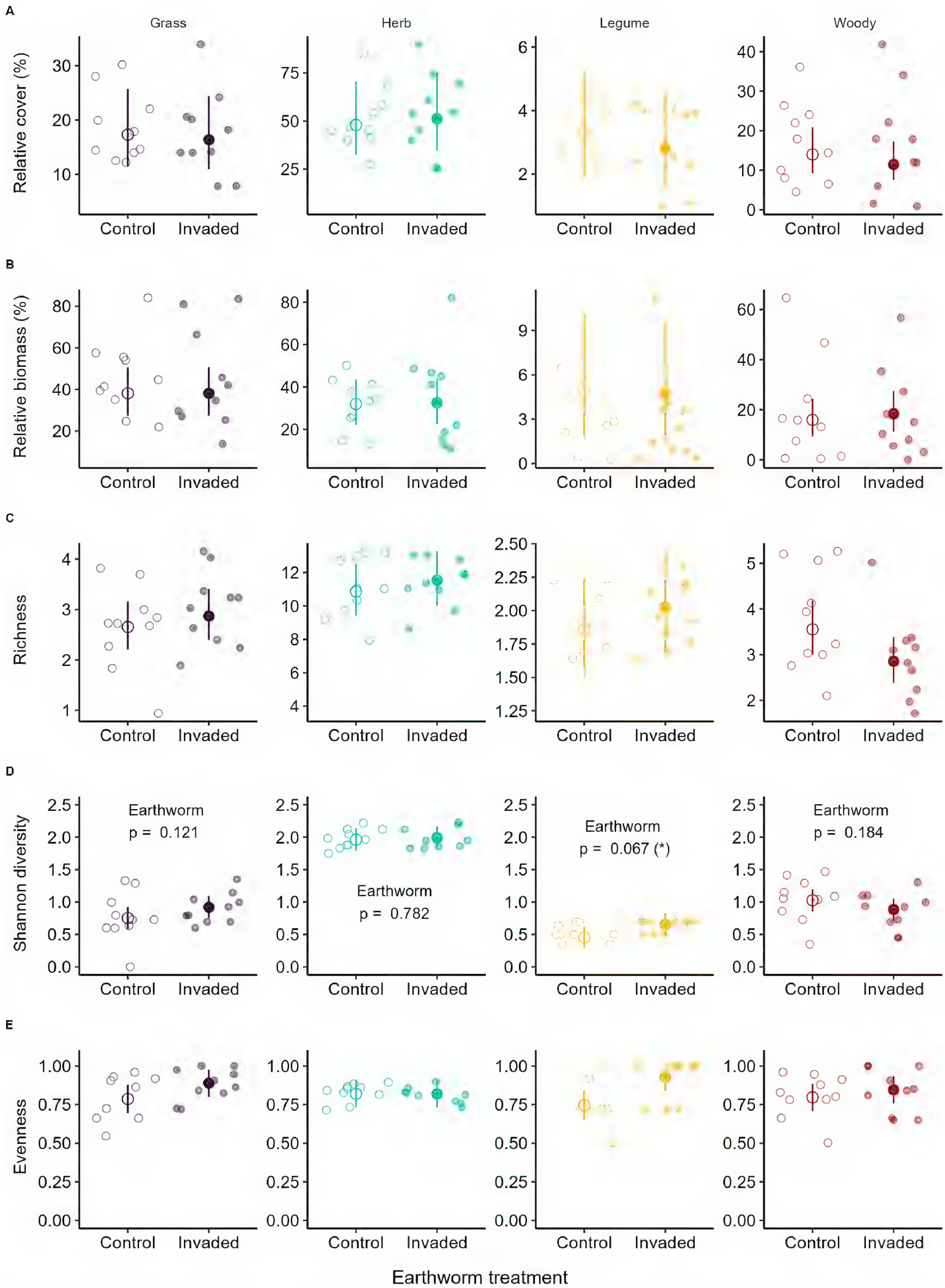

Figure 4. Effect of invasive earthworms on plant functional group productivity and diversity. The impact of invasive earthworms was measured on the relative cover (**A**), relative biomass (**B**), richness (**C**), Shannon diversity (**D**) and evenness (**E**) of the different plant functional groups. Data points (10 observations per earthworm treatment) are included in the background, with open circles for control enclosures and filled circles for invaded enclosures. Estimated marginal means and confidence intervals $CI_{95\%}$ are shown (after being back-transformed when necessary), while data points are included in the background. The p-values corresponded to the results of the post-hoc tests performed by plant functional group, when the interaction between earthworm treatment and plant functional groups was at least marginally significant in the linear models. Significance codes: (*)≤0.10.

non diversity of legumes (+43.3%) in the invaded enclosures. The Shannon diversity of legumes which was on average 0.45 in the control treatment reached 0.65 in the earthworm treatment. Moreover, the earthworm treatment alone marginally affected plant functional group evenness, with an overall higher evenness (+10.5%) in the invaded area ($F_{1.69}$=3.38, p=0.07) for the different functional groups, while there was no significant interaction between earthworm treatment and plant functional group identity ($F_{3.69}$=1.98, p=0.13, Fig. 4E). Plant community trait composition was not affected by the earthworm treatment: the CWM of plant height ($F_{1.17}$=0.07, p=0.79), as well as leaf carbon and nitrogen content ($F_{1.17}$=0.27, p=0.61 and $F_{1.17}$=0.04, p=0.84 respectively; see Suppl. material 3) did not change significantly in response to the invasive earthworm treatment, but the CWM of leaf nitrogen content decreased with an increase of canopy openness ($F_{1.17}$=7.26, p=0.015).

Effects of the invasive earthworm treatment on ecosystem functions

The soil microbial biomass was significantly lower in the deeper soil layer than in the upper soil layer ($F_{1.36}$=96.01, p<0.001, Fig. 5A) and was not affected by the earthworm treatment (alone: $F_{1.36}$=0.18, p=0.68; Interaction effect: $F_{1.36}$=0.51, p=0.48).

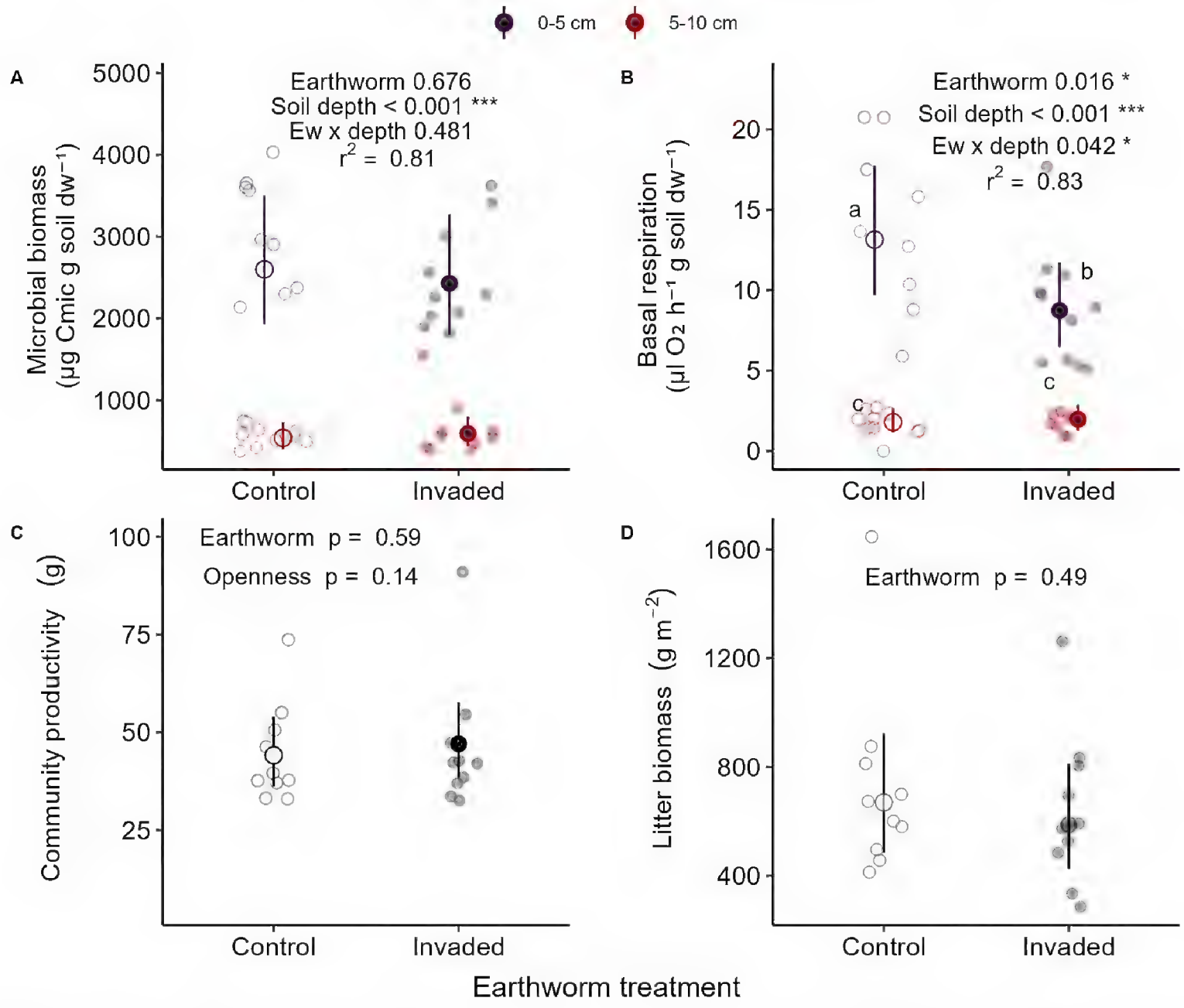

Figure 5. Effect of invasive earthworms on ecosystem functions. Soil microbial biomass (**A**) and basal respiration (**B**) according to earthworm treatment (control (open circle) vs invaded (filled circle)) and soil depth (0–5 cm (dark gray) vs 5–10 cm (brown)), as well as plant productivity (**C**) and litter biomass (**D**) according to earthworm treatment. Estimated marginal means and confidence intervals $CI_{95\%}$ are shown (after being back-transformed when necessary), while data points are included in the background. The p-values and r^2 are based on linear models. r^2 are given when at least one factor alone or in interaction was significant. Letters correspond to the results of post hoc tests performed when the interaction between earthworm treatment and soil depth was significant: different letters show significant differences between soil depth and earthworm invasion status. Number of observations per earthworm treatment and soil depth: 10. Significance codes: ***<0.001; *<0.05.

Conversely, the basal respiration of the microbial community decreased by 33.5% in the earthworm invasion treatment in the upper soil layer with values going from ~13.1 µl O_2 h^{-1} g^{-1} dry soil in the control to 8.8 µl O_2 h^{-1} g^{-1} dry soil in the earthworm treatment, but remained similar in the deeper soil layer (Interaction effect: $F_{1.35}$=4.47, p=0.04, Fig. 5B). Moreover, the earthworm treatment did not significantly affect ecosystem functions like plant community productivity ($F_{1.17}$=0.30, p=0.59, Fig. 5C) and litter biomass ($F_{1.18}$=0.50, p=0.49, Fig. 5D).

Discussion

As one of the first field experiments on the subject, our study shows that invasive earthworms altered soil abiotic properties and soil respiration already two years after the establishment of the experimental treatments. The invasion of earthworms increased soil pH in the deeper soil layer, while it decreased soil nitrogen content in the upper soil layer and decreased soil carbon across soil depths in the invaded enclosures. Furthermore, invasive earthworms reduced the difference in percentage of water-stable aggregates among soil layers that was observed in the control treatment. This change should have affected water flow in the soil (Blouin et al. 2013; Hallam and Hodson 2020), but we did not observe any invasive earthworm treatment effect on the soil water content after two years of experiment. The absence of change in the soil water content with earthworm invasion could be linked to the missing impact on the litter biomass: a high biomass of leaf litter would rather have a protective effect and limit evapotranspiration from the soil, thus keeping the water content high. These results are largely in line with literature based on observational studies. Soil chemical properties are often affected by invasive earthworms due to their feeding and burrowing activities, as highlighted in a recent meta-analysis (Ferlian et al. 2020). The burrowing activities of earthworms could be an explanation for these changes. For example, they often decrease the soil water content and induce a decrease in the soil nutrient content due to the nutrient leaching into deeper soil layers (Bohlen et al. 2004; Frelich et al. 2006; Resner et al. 2015; Richardson et al. 2018). However, we did not find any general homogenization effect of soil abiotic and biotic properties as observed in some meta-analyses (Ferlian et al. 2018, 2020): only the percentage of water-stable aggregates seems to be homogenized across the soil profile.

The earthworm community composition and biomass probably generate variability in our results of soil abiotic properties. Indeed, it is important to note that the difference between the impacts on the diverse soil properties could highlight the effect of the invasive earthworm community composition, as well as the role of the different earthworm ecological groups, as they differ in their feeding and burrowing activities. For example, anecic and endogeic species are more likely to affect the organic soil layer and drive the magnitude of the earthworm community effect, while epigeic earthworms would tend to affect the mineral soil layer (Ferlian et al. 2020). Although the results may depend on soil type, in addition to the earthworm community composition (McLean et al. 2006; Ferlian et al. 2018), the earthworm effect on soil abiotic properties could explain the decrease of soil microbial basal respiration measured in the upper soil layer in the presence of invasive earthworms, which has also been observed in other observational studies (Eisenhauer et al. 2007, 2011). The impact of invasive earthworms on soil microbes which was reviewed in McLean et al. (2006), could be due to the increase

of soil pH and nutrient stress in the upper soil layer for instance, that could have further cascading effects on soil microbial community composition and functions (Eisenhauer et al. 2011).

Moreover, the shifts in abiotic and biotic soil properties due to the experimental earthworm invasion were expected to be the reasons for the anticipated changes in plant diversity. Indeed, the decrease in nitrogen content in the upper soil layer could have led to a change in plant community structure and composition by favoring grass species that are more efficient in taking up resources from the soil (Craine et al. 2001; Craven et al. 2017; Freschet et al. 2017). However, our study only found little evidence to support such an effect after two years of this field experiment. There was no significant impact of the experimental earthworm invasion treatment on species richness, Shannon diversity, or evenness of the overall plant community, and these indices, when measured at the plant functional group level, were only slightly impacted by the invasive earthworm treatment.

While we expected a positive effect of invasive earthworms on grass species and a negative one on herb species, our results showed that the earthworm treatment had a marginally significant positive effect on the Shannon diversity of legumes, and on the evenness of all plant functional groups. To our knowledge, few observational studies have explored the effects of invasive earthworms on plant functional group diversity: only Hale et al. (2006) found that invasive earthworm biomass decreased herbaceous plant richness and Shannon diversity in some forests, while it increased it in others. As for soil abiotic and biotic properties, several authors have reported that invasive earthworm species identity and community composition played a role in the changes in the plant community composition. For instance, Hale et al. (2006) found that plant richness varied according to the composition of the earthworm community, with a stronger decrease observed when the community was dominated by the anecic species *L. terrestris.* By contrast, Holdsworth et al. (2007) observed that the presence of the epigeic *D. octaedra* tended to increase plant species richness compared to other earthworm species, even if this effect was mainly attributed by the authors to the effect of *L. terrestris* invasion on *D. octaedra* biomass. Consequently, we can assume that the mechanisms differ by which earthworm species or ecological groups affect plants (Andriuzzi et al. 2016). For example, endogeic earthworms could directly disrupt or benefit the root systems of some species, in particular, due to their higher activity in the top soil layer (Scheu 2003; Capowiez et al. 2021), while anecic earthworms would more likely impact plant species *via* their effect on nutrient re-distribution in the soil, i.e., due to the incorporation of litter nutrients but also nutrient transport into deeper soil layers. Additionally, epigeic species would rather have a limited effect on plant community (Hale et al. 2006) and belowground traits due to their limited mixing effect of mineral and organic layers by feeding on and living in litter material. We thus do not expect the colonization of the control enclosures by epigeic earthworms to have affected the results of our field experiment. This is especially the case because their biomass was rather low compared to that in the earthworm treatment (see Suppl. material 1), and because several meta-analyses (Eisenhauer 2010; Craven et al. 2017; Ferlian et al. 2018, 2020) have shown that invasive earthworm effects increased with biomass, and that epigeic earthworms typically have minor effects under the studied conditions. However, to verify these hypotheses further studies with different earthworm species, ecological groups and plant species and/or functional groups are needed.

The effect of earthworm community composition could also be a potential explanation for the slightly positive effect of invasive earthworms on legume species diversity and plant functional group evenness in the present study. The positive earthworm effect on legumes contradicts literature that mainly showed negative (Eisenhauer et al. 2007) or neutral (Wurst et al. 2003; van Groenigen et al. 2014) effects of (invasive) earthworms on the cover and biomass of legume species in the field. However, some positive effects were reported in laboratory (Eisenhauer and Scheu 2008) and field (Eisenhauer et al. 2009b) experiments using earthworm and plant species co-occurring in Central Europe. For example, Eisenhauer and Scheu (2008) as well as Wurst et al. (2003) found a positive effect of anecic or endogeic earthworms on the biomass and on the total nitrogen content of the legume *Trifolium repens*, when grown without grasses as competitors. As legume species fix atmospheric nitrogen in their nodules (rhizobium symbiosis), they are expected to be rather independent of soil nitrogen (Hirsch et al. 2001; Eisenhauer and Scheu 2008). We consequently expected them to not rely on changes in soil nutrient availability and uptake due to invasive earthworm burrowing and feeding activities. Thus, our results could suggest that the impacts of earthworms on this particular plant functional group may not be directly attributed to their effects on the legume nutrient uptake from soil. Instead, these impacts may be attributed to the decrease in the inter-specific competition resulting from the decrease in the soil nutrient content due to earthworm presence, and specifically to soil nitrogen in the upper soil layer that we observed. Another explanation could be their burrowing and mechanical activities that might alter rooting depth or distribution, promote nodules/nitrogen-fixing bacteria density (Thompson et al. 1993; Doube et al. 1994), and/or influence mycorrhizal colonization of the plants (Lawrence et al. 2003; Paudel et al. 2016). Moreover, the promotion of legume species by invasive earthworms could affect the nitrogen dynamics in the soil and have an indirect facilitative effect on some specific neighboring species via different mechanisms (Temperton et al. 2007). This effect on legumes is maybe a first and transient step toward changes in understory plant community composition and means that, before losing diversity, there might first be a change in the structure of the plant community. However, these results need to be interpreted with caution as they represent only a marginally significant trend, and further long-term experiments (i.e., longer than two years) are needed to investigate the cascading effects of invasive earthworms on plant communities.

Furthermore, after two years of this experiment, invasive earthworms did not significantly impact the relative cover and biomass of the plant functional groups, despite evidence from existing literature (Hale et al. 2006; Paudel et al. 2016; Craven et al. 2017). For instance, studies by Nuzzo et al. (2009) and Holdsworth et al. (2007) reported a decrease in the herb, forb, and woody species cover with an increase of invasive earthworm biomass, while sedge or grass cover increased (Holdsworth et al. 2007; Drouin et al. 2016). The lack of change in plant species cover and biomass in our study could explain the absence of effects of invasive earthworms on the plant community-weighted means of height, leaf carbon, and nitrogen contents after two years of treatment. Indeed, if there is no change in plant community and functional group composition/dominance, it is unlikely to see changes in plant community trait composition, and thus in ecosystem functions like productivity and litter decomposition. We did not observe higher productivity or an accelerated litter decomposition due to changes in plant community traits (such as lower height and carbon

content, and higher nitrogen content), attributed to the dominance of grass species in the community as we expected in the presence of invasive earthworms compared to the control enclosures. Additionally, an explanation for missing differences in the litter biomass between treatments could be that the large amount of litter that had accumulated across years before earthworm invasion, is slowly decomposed by the earthworm community, with these effects not yet being visible. These potential effects on plant community composition, traits, and ecosystem functions could thus need more time to materialize. Time-delayed responses from plant functional groups and communities to earthworm invasion were, to our knowledge, not investigated so far. It is probably due to the difficulties to report the time since the establishment of the invasive earthworm community in observational approaches and thus the challenge to investigate potential time lags in the response of the plant community after earthworm community establishment. Despite these difficulties, we stress the need to further investigate the sequence and timing at which changes occur, and when the effects of invasive earthworms on soil properties and their cascading effects on plant communities take place, to better understand the mechanisms behind plant community and ecosystem function changes after the invasion.

Moreover, the time since establishment of the earthworm community itself might have affected our results: the maximum ecological effects of the earthworm community on soil properties, communities, and ecosystem functions might need more time to materialize. Consequently, our study reinforces the idea of a sequence of events, and ecological cascade following earthworm invasion (Frelich et al. 2019), with the first effect of earthworm invasion being to alter soil structure and nutrient availability, as well as microbial activity, mainly in the upper soil layer. Our study also suggests that invasive earthworm effects on plant communities are mainly mediated by changes in soil properties (i.e., indirect effects), while proposed direct effects on plants (e.g., via interactions with seeds and seedlings) may have played a minor role.

Notably, we would like to stress that the present approach of introducing invasive species into an uninvaded area of the forest may slightly facilitate the spread of invasive species. As a word of caution, such work needs to be well planned, should be based on extensive knowledge on the study location and invasive species, and has to be supported by local authorities with the respective permits. Based on careful planning and transparent communication, we received the required permits by local authorities. The invasion of this forest by earthworms has been studied intensively across the last three decades (e.g., Scheu and Parkinson 1994; Eisenhauer et al. 2007; Straube et al. 2009; Jochum et al. 2022), which is why there is solid empirical evidence for the proceeding invasion of the forest and the moving invasion front. Notably, we only selected invasive earthworm species that had already been present in this forest for many years, and set up the experiment in an area of the forest that, based on this previous research, would experience earthworm invasion within a couple of years. As mentioned in the Methods section, some epigeic earthworms even colonized some control enclosures during our experiment, which also reflects the speed of the invasion in this area. Moreover, at the end of the experiment, we returned our research site as much as possible to pre-existing conditions, following Alberta Parks' protocols and recommendations. To do so, we removed the metal sheets of the enclosures using equipment cleaned beforehand to reduce the spread of invasive species. We also replaced/returned native vegetation plots and added native leaf litter on any areas of bare soil to reduce the potential of invasive species/weed establishment.

Conclusions

Our experimental field study shows that invasive earthworms significantly alter soil abiotic properties (i.e., soil nutrient contents, pH, water-stable aggregates) after two years, but without having strong consequences for plant taxonomic diversity, yet. Invasive earthworms slightly affected the Shannon diversity of legumes and the evenness of plant functional groups. These are potentially the first signs of the effects of invasive earthworms on plant communities that have been reported from observational studies (Holdsworth et al. 2007; Nuzzo et al. 2009; Alexander et al. 2022). However, in our two-year field experiment, invasive earthworms did not affect the relative cover and biomass of particular plant functional groups, yet, which has to be linked to the lack of changes in the plant community-weighted mean trait values, and the ecosystem functions studied, i.e., plant community productivity and litter decomposition that remained unaffected after two years of invasion. Our study suggests that the impacts of invasive earthworms on plant communities and ecosystem functioning are likely to become apparent after two years of invasion. These findings underscore the significant impacts of invasive earthworms on soil abiotic and biotic properties (Ferlian et al. 2020) that may then cascade to influence biological communities above and below the ground (Frelich et al. 2019; Jochum et al. 2022) and highlight the time lags in the response of the plant community to the establishment of invasive earthworms.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: LT, NE. Methodology: LT, NE. Investigation: LT, LH, OF, MJ. Formal analysis: LT, LH. Resources: NE. Data curation: LT. Writing- original draft: LT. Writing-review & editing: LT, NE, MJ, OF, LH. Visualization: LT. Supervision: LT, NE. Funding acquisition: LT, NE.

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Data availability

The data and code are publicly available on the data repository Zenodo https://doi.org/10.5281/zenodo.11395032 (Thouvenot et al. 2024b).

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Supplementary material 1

Description of the invasive earthworm treatment

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Supplementary material 2

Plant community composition

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Supplementary material 3

Plant community traits

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Data type: docx

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